Competition-density effect in plant populations

XUE Li
(College of Forestry, South China Agriculture University, Guangzhou 510642, P. R. China)

Abstract: The competition-density effect of plant populations is of significance in theory and practice of forest management and has been studied for long time. The differences between the two reciprocal equations of the competition-density effect in nonself-thinning populations and self-thinning populations were analyzed theoretically. This supplies a theoretical basis for analyzing the dynamics of forest populations and evaluating the effect of forest management.

Keywords: Competition-density effect; Self-thinning population; Nonself-thinning population
CLC number: S711 **Document code:** A **Article ID:** 1007-662X(2002)01-0048-03

Introduction

The relationship between mean plant weight and density has long been regarded as important phenomenon from both theoretical and practical viewpoints. Two basic contents have been revealed from their relationship. The first is the competition-density (C-D) effect, which refers to the relationship at a particular moment in time between mean plant weight and density among populations grown at different levels of density, and the second is self-thinning, which refers to the time-trajectory of mean plant size and density along a time continuum. Shinozaki and Kira (1956) proposed the reciprocal equation of the C-D effect, which provides an accurate description of mean plant weight-density relationship. Several reciprocal equations for describing the C-D effect have been developed (Bleasdale and Nelder 1960; Nelder 1962; Bleasdale 1967; Farazdaghi and Harris 1968; Watkinson 1980, 1984; Vandermeer 1984). These equations originate in the logistic theory of the C-D effect established by Shinozaki and Kira (1956). Since the logistic theory is concerned with non-self-thinning stands, there would be a theoretical limit in reconciling the C-D effect and self-thinning within the framework of the logistic theory of the C-D effect (Minowa 1982; Naito 1992). Hagihara (1996, 1999) constructed a model for describing the C-D effect in self-thinning stands in line with the logistic theory of the C-D effect.

This paper discussed the theories of the C-D effects in nonself-thinning and self-thinning plant populations are presented, and the differences between the two theories.

The C-D effect in non-self-thinning plant populations

Shinozaki and Kira (1956) established the logistic theory of the C-D effect, the theory is constructed from the following assumptions:

Assumption 1: The growth of mean plant weight w follows the general logistic equation,

$$\frac{1}{w}\frac{\mathrm{d}w}{\mathrm{d}t} = \lambda(t)\left(1 - \frac{w}{W(t)}\right) \tag{1}$$

where $\lambda(t)$ is the coefficient of growth and $W(t)$ is the asymptote of w.

Assumption 2: The coefficient of growth $\lambda(t)$ is independent of density ρ,

$$\frac{\partial \lambda(t)}{\partial \rho} = 0 \tag{2}$$

Assumption 3: The final yield $Y(t)$ is independent of ρ (Kira *et al.*,1953),

$$W(t) = \frac{Y(t)}{\rho} \tag{3}$$

$$\frac{\partial Y(t)}{\partial \rho} = 0 \tag{4}$$

Assumption 4: Initial mean plant weight w_0 is independent of ρ,

$$\frac{\partial w_0}{\partial \rho} = 0 \tag{5}$$

On the basis of these assumptions, the following reciprocal equation of the C-D effect in nonself-thinning plant populations is derived,

$$\frac{1}{w} = A\rho + B \tag{6}$$

where A and B are coefficients at a given growth stage, and the coefficients A and B are respectively defined as,

Biography: XUE Li (1958-), male, Ph. Doctor, associate professor in College of Forestry, South China Agriculture University, Guangzhou 510642, P. R. China. E-mail: forxue@scau.edu.cn
Received date: 2001-12-14
Responsible editor: Song Funan

$$A = e^{-\tau} \int_0^{\tau} \frac{e^{\tau}}{Y(t)} d\tau \tag{7}$$

and

$$B = \frac{e^{\tau}}{w_0} \tag{8}$$

where initial mean plant weight w_0 is independent of density ρ, and τ is called biological time (Shinozaki 1961) defined as the integral of $\lambda(t)$ with respect to physical time t:

$$\tau = \int_0^t \lambda(t) dt \qquad \text{or} \qquad d\tau = \lambda(t)\, dt \tag{9}$$

Equation (6) is called the reciprocal equation of the C-D effect (Shinozaki and Kira 1956), which describes the relationship between mean plant weight w and density ρ in nonself-thinning stands.

The C-D effect in self-thinning plant populations

Hagihara (1996,1999) has developed the logistic theory of the density effect in self-thinning populations in line with the logistic theory of the C-D effect proposed by Shinozaki and Kira (1956). His theory consists of the following five assumptions:

Assumption 1: The growth of yield per unit area y follows the general logistic equation,

$$\frac{1}{y}\frac{dy}{dt} = \lambda(t)\left[1 - \frac{y}{Y(t)}\right] \tag{10}$$

where $Y(t)$ is the upper limit of y, which is dependent on time t.

Assumption 2: The coefficient of growth $\lambda(t)$ is independent of initial density ρ_i,

$$\frac{\partial \lambda(t)}{\partial \rho_i} = 0 \tag{11}$$

Assumption 3: The final yield $Y(t)$ is independent of ρ_i,

$$\frac{\partial Y(t)}{\partial \rho_i} = 0 \tag{12}$$

Assumption 4: Initial mean plant weight w_0 is independent of ρ_i,

$$\frac{\partial w_0}{\partial \rho_i} = 0 \tag{13}$$

Assumption 5: The relationship between realized density ρ and initial density ρ_i is given by following equation (Shinozaki and Kira 1956),

$$\frac{1}{\rho} = \frac{1}{\rho_i} + \varepsilon \tag{14}$$

where ε is a coefficient independent of both ρ and ρ_i, but is a function of time. The reciprocal of ε represents the asymptotic density at a given time.

These assumptions lead to the reciprocal equation of the C-D effect in self-thinning populations being expressed as,

$$\frac{1}{w} = A_t \rho + B \tag{15}$$

where w is the mean plant weight (= y/ρ), and the coefficient A_t and B are respectively defined as,

$$A_t = e^{-\tau} \int_0^{\tau} \frac{e^{\tau}}{Y(t)} d\tau - \varepsilon \frac{e^{-\tau}}{w_0} \tag{16}$$

and

$$B = \frac{e^{-\tau}}{w_0}$$

Equation (15) is called the reciprocal equation of the C-D effect in self-thinning populations, which describes the relationship between mean plant weight w and density ρ in self-thinning stands.

Discussion

If the density ρ is maintained at a constant value (i.e. in the state of initial density ρ_i throughout the experiment), then Eq. (15) reduces to

$$\frac{1}{w} = A\rho + B$$

In the logistic theory of the C-D effect, the mean plant weight w assumed to follow the general logistic equation in Assumption 1 and the final yield $Y(t)$ was defined as $W(t)$ ρ, where $W(t)$ is the upper limit of w, in Assumption 3. Assumptions 2 and 4 in the logistic theory of the C-D effect in self-thinning populations are basically the same as those in the logistic theory of the C-D effect. Assumption 5 is newly incorporated into the logistic theory of the density effect in self-thinning populations. The coefficient A_t in Eq. (15) is quite different from the coefficient A in Eq. (6). Considering Eqs. (7), (8) and (16), it follows that A_t is equal to the sum of A and $-\varepsilon B$.

The C-D effect in self-thinning populations consists of two components: competition by surviving trees and morality of some trees. With tree growth, the competition will become

violent, whereas morality of some trees will alleviate the competition. These two opposing processes always exist during the whole period of tree growth. Equation (15) theoretically harmonizes the C-D effect observed at a fixed time with the self-thinning observed along a time continuum.

Equation (6) fairly well explained the C-D effect of the nonself-thinning populations of herbaceous plant (Shinozaki and Kira, 1956), *Larix leptolepis* (Fang *et al.* 1991), *Cunninghamia lanceolata* and *Pinus massoniana* (Xue and Hagihara, 2001a,b) and Eq. (15) succeeded in analyzing the growth characteristics and dynamics of self-thinning populations of *Pinus densiflora* and *Pinus massoniana* (Xue and Hagihara, 1998, 1999, in press), indicating that the two theoretical models can provide tools for analyzing the dynamics of population growth.

References

Bleasdale, J.K.A. 1967. The relationship between the weight of a plant part and total weight as affected by plant density [J]. Journal of Horticultural Science, **42**: 51-58.

Bleasdale, J.K.A., Nelder, J.A. 1960. Plant population and crop yield [J]. Nature, **188**: 342.

Fang Jingyun, Kan, M., Yamakura, T. 1991. Relationships between population growth and population density in monocultures of *Larix leptolepis* [J]. Acta Botanica Sinica, **33**: 949-957 (in Chinese).

Farazdaghi, H. and Harris, P.M. 1968. Plant competition and crop yield [J]. Nature, **217**: 289-290.

Hagihara, A. 1996. Logistic theory of the density effect in self-thinning populations [J]. Bulletin of the Nagoya University Forest, **15**: 31-50 (in Japanese).

Hagihara, A. 1999. Theoretical considerations on the C-D effect in self-thinning plant populations [J]. Research of Population Ecology, **41**: 151-159.

Kira, T., Ogawa, H., Shinozaki, K. 1953. Intraspecific competition among higher plants. I. Competition-yield-density interrelationship in regularly dispersed populations [J]. Journal of Institute of Polytechnics, Osaka City University, D **4**:1-16.

Minowa, M. 1982. A theoretical approach to forest growth model. I. The log-Mitscherlich theory [J]. Journal of the Japanese. Forestry Society, **64**: 461-467 (in Japanese).

Naito, K. 1992. Studies on forest growth modeling [J]. Bulletin of Utsunomiya University Forest, **28**: 1-95 (in Japanese).

Nelder, J.A. 1962. New kinds of systematic designs for spacing experiments [J]. Biometrics, **18**: 283-307.

Shinozaki, K. 1961. Logistic Theory of Plant Growth [D]. Doctoral Thesis, Kyoto Univ., Kyoto (in Japanese).

Shinozaki, K., Kira, T. 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect [J]. Journal of Institute of Polytechnics, Osaka City University, **D 7**: 35-72.

Vandermeer, J. 1984. Plant competition and the yield-density relationship [J]. Journal of Theoretical Biology, **109**: 393-399.

Watkinson, A.R. 1980. Density-dependence in single-species populations of plants [J]. Journal of Theoretical Biology, **83**: 345-357.

Watkinson, A.R. 1984. Yield-density relationships: the influence of resource availability on growth and self-thinning in populations of *Vulpia fasciculate* [J]. Annals of Botany, **53**: 469-482.

Xue Li, Hagihara, A. 1998. Growth analysis of the self-thinning stands of *Pinus densiflora* Sieb. *et* Zucc [J]. Ecological Research, **13**: 183-191.

Xue Li, Hagihara, A. 1999. Density effect, self-thinning and size distribution in of *Pinus densiflora* Sieb. *et* Zucc. Stands [J]. Ecological Research, **14**: 49-58.

Xue Li, Hagihara, A. 2001a. Growth analysis on the competition-density effect in Chinese fir (*Cunninghamia lanceolata*) and Masson pine (*Pinus massoniana*) stands [J]. Forest Ecology Management, **150**: 331-337.

Xue Li, Hagihara, A. 2001b. Growth analysis on the competition-density effect in *Cunninghamia lanceolata* stands [J]. Chinese Journal of Applied Ecology, **12**: 171-174 (in Chinese).

Xue Li, Hagihara, A. Growth analysis on the C-D effect in self-thinning Masson pine (*Pinus massoniana*) stands [J]. Forest Ecology Management (in press).